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External and Middle Ear Characteristics of Primates, With Reference to Tarsier-Anthropoid Affinities

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ABSTRACT

Otic anatomy has been used to propose two different hypotheses about tarsier-anthropoid affinities: (1) *Tarsius* and Anthroipoidea evolved independently from Paleogene omomyid tarsoids, and (2) *Tarsius* (or Tarsiidae) and Anthroipoidea are phyletic sister groups. The arrangement of otic structures into form-function complexes of the middle and external ear is essential for phylogenetic analysis. Although the middle ear cavities in anthropoids contain mastoid cells not present in *Tarsius*, the two taxa share tympanic and anterior accessory cavities in a dual cavity-septum configuration. The resonant effects of the two coupled volumes are closely similar in *Saimiri* and *Tarsius* despite marked differences in the position of the septum and aditus, suggesting that their middle ear morphology is convergent. Although the intrapetrous pathway of the internal carotid artery has been described as “perbullar” in both anthropoids and *Tarsius*, the artery crosses part of the

tympanic cavity (promontory) in platyrrhines but not in *Tarsius*. Furthermore, a branch of the tympanic nerve passes through the carotid foramen in at least some anthropoids but not the anterolaterally-shifted carotid foramen of *Tarsius*. The emergence of the internal carotid nerve onto the *external* aspect of the promontorial canal in tupaiids and probably *Rooneyia viejaensis* supports Szalay's (1975a) contention that a large promontorial artery links omomyids with living haplorhines. The bony external meatal tube is an adaptation designed to reduce physiological noise in species where the jaw joint borders directly on the external ear. Since the bony meatal tube is characteristic of the rounded and clinocranial skull of *Tarsius*, the skull of the earliest anthropoids probably did not closely resemble those of *Tarsius* or Paleogene forms currently recognized as “tarsioid.”

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INTRODUCTION

The auditory region is of focal paleontological interest because it provides many separately describable anatomical characters considered useful for proposing hypotheses about evolutionary relationships. Two current hypotheses concerning the affinities of tarsiid and anthropoid primates are: (1) *Tarsius* and Anthropoidea evolved independently from Paleogene omomyid tarsioids (Szalay, 1975a, 1975b, 1976; Rosenberger and Szalay, 1980), and (2) *Tarsius* (or Tarsiidae) and Anthropoidea are phyletic sister groups, which share a more recent common ancestor with each other than with any omomyid (Cartmill and Kay, 1978; Cartmill, MacPhee, and Simons, 1981). These hypotheses were based on different morphological interpretations (character analyses) of the intrapetrotal pathway of the internal carotid artery, the organization of the principal spaces and septa of the middle ear, the relative sizes of the promontorial and stapedial branches of the internal carotid artery, and the structure of the external auditory meatus. The primary goal of this study is to contribute to the evolutionary interpretation of these otic structures through a consideration of middle and external ear function. As pointed out by Simpson (1961), all one can do at the morphological (observational) level is to describe the details of existing similarities. A consideration of the functional properties of features allows a more complete assessment of the systematic importance (e.g., homology or analogy) of morphological variations among species (see Bock, 1981).

Omomyid auditory regions are best known from the well-preserved skulls of *Necrolemur antiquus* (Hurzeler, 1948; Simons, 1961; Szalay, 1975a, 1975b, 1976) and *Rooneyia viejaensis* (Szalay and Wilson, 1976; Szalay, 1976). Szalay (1975a, 1976), Szalay and Wilson (1976), and Rosenberger and Szalay (1980) considered an omomyid-*Tarsius*-anthropoid clade to be tied together by a posteromedial position of the posterior carotid foramen, a relatively large internal carotid (promontorial) artery, and a relatively small stapedial artery. Artery size estimates for fossil forms are based on measurements of bony

arterial canals on the promontory in the middle ear (see Results). Thus, the carotid arterial pattern was viewed as a shared derived character of these taxa when compared with the condition seen in lemuroids.

On the other hand, Cartmill and Kay (1978) and Cartmill, MacPhee, and Simons (1981) considered the so-called peribullar³ pathway of the internal carotid artery to be a synapomorphy of a *Tarsius*-anthropoid clade when compared to the primitive transpromontorial pathway characteristic of omomyids and other Paleogene prosimians. In addition, at least part of the bony canal for the internal carotid artery develops from the petrosal plate in *Tarsius* and anthropoids. The petrosal plate also forms a transverse bony septum which separates the tympanic cavity proper from an anterior accessory cavity. Although the middle ear of *Necrolemur* has a dual cavity arrangement with an enlarged mastoid cavity, the dual cavity-septum configuration is not present in known omomyids. The medial entry position of the internal carotid artery cited by Szalay (1975a) as a shared derived character of omomyids and anthropoids was shown to be a primitive primate character providing no evidence of special affinity (Cartmill, MacPhee, and Simons, 1981; MacPhee, 1981).

These authors also emphasized that omomyids resemble other Paleogene prosimians, but differ from *Tarsius* and anthropoids, in having a subtymppanic extension of the tympanic cavity (hypotympanic fossa). The hypotympanic fossa is formed when the tympanic ring (ectotympanic) is "intrabullar" and connected to the meatal rim of the bulla by an "anular bridge." This anular bridge is ossified in omomyids and membranous in lemuriforms (see MacPhee, 1977), whereas the ectotympanic ring fuses directly to the bulla wall in *Tarsius* and anthropoids. For these reasons, Cartmill and Kay (1978) regarded *Tarsius* as the closest known tarsiiform relative of anthropoids, and refused to include omomyids in the suborder Haplorhini.

³ Running between the tympanic and anterior accessory cavities in subvertical orientation.

The systematic interpretation of meatal structures has been bedeviled by the fact that the position of the tympanic ring relative to the bulla wall is not correlated with the length of the bony portion of the meatus. Oromyids and *Tarsius* share a bony meatal tube extending laterally beyond the recessus meatus, whereas New World anthropoids and the oldest known Old World anthropoids are characterized by a bony meatus limited to a simple ringlike ectotympanic (Szalay and Wilson, 1976; Gingerich, 1973; Hershkovitz, 1974; Cartmill, MacPhee, and Simons, 1981). Cartmill, MacPhee, and Simons (1981) discount this trait as "highly labile," implying that the bony meatal tube neither closely links oromyids with *Tarsius* nor invalidates the sister group status of *tarsiids* and anthropoids. We propose a functional explanation for the bony meatal tube which has broad implications for the systematic interpretation of meatal structures.

ACKNOWLEDGMENTS

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FIGURE ABBREVIATIONS

AA, anterior aditus; AB, auditory bulla; AT, auditory tube; BMF, bony meatal flange; BMT, bony meatal tube; CC, carotid canal; CCA, common carotid artery; CIN, canal for internal carotid nerve; EAM, external auditory meatus; ECA, external carotid artery; FM, foramen magnum; FO, fenestra vestibuli (oval window); FR, fenestra cochleae (round window); GF, glenoid fossa; HC, hypoglossal canal; I, incus; ICN, internal carotid nerve; JF, jugular fossa; M, malleus; MC, mandibular condyle; OA, occipital artery; P, promontory; PC, canal for promontorial artery; PGF, postglenoid foramen; PGP, postglenoid process; PSR, pre-septal recess

of tympanic cavity; RSA, remnant stapedial artery; S, stapes; SC, canal for stapedial artery; SCG, superior cervical ganglion; TC, tympanic canaliculus; TN, tympanic nerve; TS, transverse septum; IX, glossopharyngeal nerve; X, vagus nerve; XII, hypoglossal nerve.

MATERIALS AND METHODS

Ear regions of *Tarsius syrichta* (three specimens), *Tupaia glis* (two specimens), *Aotus trivirgatus* (two specimens), and *Lagothrix lagotricha* (one specimen) were dissected using a Wild microscope with zoom lens. Our purpose was to determine the route and relations of the carotid arteries, the internal carotid nerve, and the tympanic nerve (of Jacobson). Canals, grooves, and foramina associated with the soft anatomy were used to identify artery and nerve routes in a larger sample of skulls. The skulls of these species and a large number of other placental and marsupial mammals were studied at the American Museum of Natural History, New York and the United States National Museum, Smithsonian Institution, Washington, D.C.

The following fossil skulls were examined to verify their middle and external ear anatomy: *Rooneyia viejaensis* (TMM 40688-7), *Notharctus tenebrosus* (AMNH 11466), *Smilodectes gracilis* (USNM 21815), *Mahgarita stevensi* (TMM 41578-9), and *Adapis magnus* (PU 11481).

Volumetric measurements of the middle ear cavities were made with a 10 μ l syringe, and water and metric measurements were made using a microscope equipped with a digital caliper (see Appendix).

RESULTS

MIDDLE EAR STRUCTURE: In this section we compare and contrast middle ear structure and function in *Tarsius* and anthropoids. Partly because the earliest known anthropoid auditory regions resemble those of New World forms in most respects (Gingerich, 1973; Hershkovitz, 1974; Szalay and Delson, 1979; Cartmill, MacPhee, and Simons, 1981), platyrrhines were chosen for comparison. Cartmill, MacPhee, and Simons (1981) pointed out that in *Tarsius* and anthropoids the carotid canal does not come

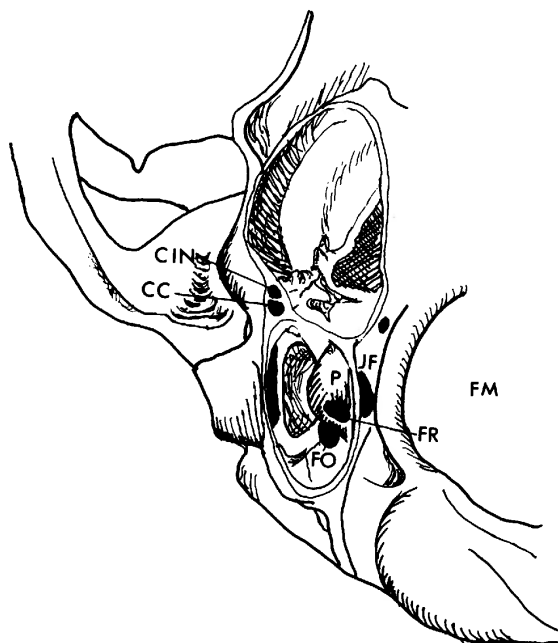


FIG. 1. Ventral view of ear region of *Tarsius* with bulla open. Note absence of trabeculae (cellules) in anterior accessory cavity and vertical orientation of transverse septum and carotid canal. There is a separate foramen and bony tube for the internal carotid nerve. Foramen (anterior aditus) in septum on lateral side of carotid canal (not visible) couples the two cavities (modified after Szalay, 1976).

into close relation with the fenestra cochleae, in contrast to omomyids and other Paleogene prosimians in which the carotid canal passes close to ("shields") the fenestra cochleae and crosses the long axis of the promontory. In *Tarsius*, the carotid canal develops from the petrosal plate and runs in vertical orientation along the *anterior cavity* surface of the transverse septum where it is completely detached from the promontory (fig. 1). In platyrrhines, however, the artery travels in a deep, inclined sulcus along the anteroventral surface of the promontory (periotic), and the petrosal plate forms only the floor and sidewall of the bony canal. The transverse septum runs from the lateral wall of the bulla to the anterior edge of the canal. In this respect, the artery passes through the tympanic cavity proper, unlike in *Tarsius* (see fig. 2).

The carotid canal is closely associated with

a transverse septum formed by the petrosal plate in both *Tarsius* and anthropoids (Cartmill, MacPhee, and Simons, 1981). In *Saimiri sciureus* the tympanic floor slopes upward anteriorly, but does not reach the tegmental wall. This part of the tympanic floor forms the transverse bony septum which helps to separate the tympanic cavity from the anterior accessory cavity. The narrow aperture remaining between the transverse septum and the tympanic roof has the carotid canal (promontory) as its medial wall and the anterior crus of the ectotympanic as its lateral wall. In some *Saimiri* the transverse septum continues anteriorly in horizontal orientation and ends as a free edge in the accessory cavity. The horizontal part is actually the floor of a foramen passage which couples the two middle ear cavities. Since the septum restricts the size of the foramen passage (see below and Appendix), its width depends upon the amount of middle ear inflation in the region of the promontory anterior pole. The septum is very narrow in *Saimiri*. Other *Saimiri* (e.g., AMNH 93675) more closely resemble the slightly different morphology in *Aotus trivirgatus* (fig. 2) and *Cebus*. Here the aperture leads into an irregular small chamber we are calling the pre-septal recess of the tympanic cavity, which in turn communicates with the anterior accessory cavity through a foramen (anterior aditus) and the outside air through the eustachian tube (fig. 2).

This morphology is significantly different from that of *Tarsius*. In *Tarsius*, the vertical septum extends across the entire width of the bulla cavity at the level of the promontory anterior pole, and is solely responsible for separating the tympanic and anterior accessory cavities (fig. 1). The two cavities are coupled by a foramen in the septum in contrast to the complicated foramen passage seen in most platyrrhines (cf. Rosenberger and Szalay, 1980). In addition, the tarsier accessory cavity is non-trabecular (lacks cellules), whereas cavity trabeculation is inversely related to body size among platyrrhines.

The width and probably the orientation of the transverse septum (anterior tympanic floor) in platyrrhines is dependent upon pneumatic activity. For example, in some *Ateles belzebuth* the carotid canal abuts against the anterior crus of the ectotympanic

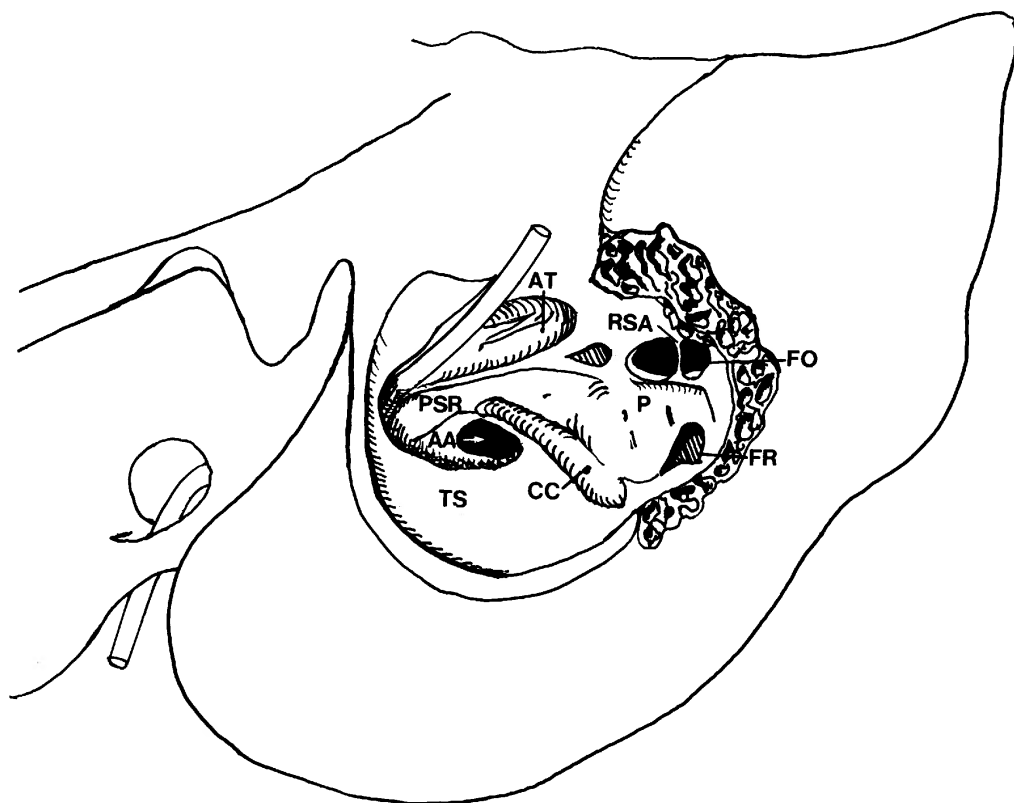


FIG. 2. Middle ear of *Aotus* viewed through external auditory meatus with ectotympanic and parts of tympanic cavity floor and mastoid removed. The obliquely oriented carotid canal can be seen protruding into tympanic cavity from bulla floor. Canal floor and lateral wall are derived from petrosal plate as in *Tarsius*, but floor is a groove in the cochlear promontory (periotic) as in Paleogene prosimians. Transverse septum and pre-septal recess are relatively broad due to middle ear inflation. In *Saimiri* the narrow pre-septal recess leads into anterior aditus and forms a narrow foramen passage between the two cavities. A possible remnant of stapedial artery (or canal) can be seen passing between crura of the stapes. A similar structure was identified bilaterally in four of 15 *Aotus* skulls. It also occurs occasionally in *Callicebus*.

because of the limited course of middle ear inflation. The septum is thus greatly restricted or absent altogether. The foramen leading into the anterior accessory cavity proper is in a horizontal plate of bone, ventral to a pre-arterial recess (compare pre-septal recess above) of the tympanic cavity. At the other extreme, the septum is relatively wide in callitrichids and the small cebids *Callicebus* and *Callimico* due to the relative expansion of the middle ear cavities (fig. 3). Smaller platyrrhines need relatively greater middle ear inflation, because the cavity volume influences hearing sensitivity at low frequencies where the middle ear impedance is compliance-dominated (see Appendix). The more

vertical placement of the internal carotid artery in callitrichids also appears to be a part of the pneumatization process, since the presence of the carotid canal in the bulla floor would restrict the ventral expansion of the tympanic cavity. As a result, resemblances to *Tarsius* are closer when the *Tarsius*-sized callitrichids are compared.

The tympanic and anterior accessory cavities can be represented as two coupled volumes, although the trabeculae (cellules) in the anthropoid accessory cavity may suggest a more complicated model. The middle ear volumes represent acoustic compliances which are coupled by the mass and resistance of the foramen passage. Series and parallel

combinations of these acoustic elements produce cavity resonances. In the Appendix we have shown that middle ear volume, foramen (anterior aditus) dimensions, and thus the resonant frequencies of the cavities are essentially the same in *Tarsius* and *Saimiri*. This is so despite marked differences in the construction of the foramen passage (and the internal carotid pathway). Since these differences are not due to the cavity or foramen dimensions, or species differences in the contribution of these cavities to the frequency selectivity of the middle ear, we conclude that the dual cavity-septum configurations in *Tarsius* and anthropoids are probably convergent⁴ specializations. We base this conclusion on the observation that the middle ears of *Saimiri* and *Aotus* are more typical of the basic ceboid plan than that of the dwarfed callitrichids. In anthropoids there should also be resonances associated with the aditus ad antrum and the small mastoid cavity at slightly higher frequencies. It is conceivable that *Tarsius* and anthropoids simply occupy different positions along the same morphocline (MacPhee and Cartmill, in press), but this is by no means certain.

The dual cavity-septum configuration affects the response of the middle ear in the middle frequencies (Dallos, 1973; Lynch, 1981). Furthermore, behavioral sensitivity is largely determined by the properties of the middle ear in this frequency range (Dallos, 1973; Lynch, Nedzelnitsky, and Peake, 1982). The effect of the cavity resonances can be seen in measurements of middle ear impedance and auditory behavioral thresholds in cats and guinea pigs (Dallos, 1973; Lynch, 1981; Zwislocki, 1963), both of which show variations on the dual cavity-septum configuration. For example, a relative minimum in the transfer function of the middle ear of the cat near 4 kHz corresponds to an upward notch (reduced sensitivity) in the 4 kHz region of the cat audiogram (Dallos, 1973). Increased sensitivity at the lower frequency of

the series resonance may not be seen in audiograms because threshold sound pressure is already decreasing in this region and the test tones are usually presented only at octave intervals. The series resonance is clearly seen as a local maximum in the middle ear admittance magnitude and a zero degree phase angle at about 2125 Hz in cats (Lynch, 1981). In these respects, the effect of the inflated mastoid cavity and aditus ad antrum in *Homo* and probably *Necrolemur* is qualitatively similar to the effect of the anterior accessory cavity and anterior aditus in other anthropoids and *Tarsius* (cf. Guinan and Peake, 1967).

A 4 kHz notch is seen in the threshold curves of *Saimiri sciureus* (Beecher, 1974a), *Aotus trivirgatus* (Beecher, 1974b), *Callithrix jacchus* (Seiden, 1958, cited by Stebbins, 1971), and several cercopithecines (Stebbins, Green, and Miller, 1966; Stebbins, 1978). It is also seen in the threshold curve of the lorises *Perodicticus potto* (Heffner and Masterton, 1970). The middle ear cavities of lorises can be represented as two coupled volumes. However, audiograms for two bushbabies (*Galago senegalensis*) do not show a well-defined 4 kHz notch (see Heffner, Ravizza, and Masterton, 1969b). One bushbaby showed a pronounced notch centered at 1 kHz. The effect of the cavities may be smaller in *Galago senegalensis* or the cavity resonance may occur at a lower frequency. The parallel resonance frequency of the human cavities is about 2 kHz (Rabinowitz, 1981), and the effect of the large cavities is relatively small (Guinan and Peake, 1967).

The 4 kHz notch is not seen in the threshold curves of species with no accessory middle ear cavities. These species include *Delphis virginianus* (Ravizza, Heffner, and Masterton, 1969a), *Hemiechinus auritus* (Ravizza, Heffner, and Masterton, 1969b), *Tupaia glis* (Heffner, Ravizza, and Masterton, 1969a), and some *Lemur catta* and *Lemur macaco* (Mitchell, Gillette, Vernon, and Herman, 1970). However, one of two *Lemur catta* and two of four *Lemur macaco* showed an anomalous broad reduction in sensitivity centered at 4 kHz. With the ossicles in place, some middle ears of *Lemur* (e.g., AMNH 170740) clearly show a narrow, slitlike foramen between the tympanic cavity and a

⁴ Since we are not certain of the antecedent forms of the two taxa, it is difficult to decide whether the similar characters are due to convergence or parallelism. Convergence emphasizes the development of similarities on the basis of shared function rather than the (unknown) characteristics of a common ancestry.

fairly large epitympanic recess. Variation in the size and shape of these spaces could account for the variation in the audiometric data because the large volume of the tympanic cavity exclusive of the epitympanic recess (about 0.7 cc) would place the parallel resonance near 4 to 5 kHz. Gregory (1920) referred to the fissure lying between the promontory and the ectotympanic bone in *Notharctus* as a "pneumatic foramen" coupling the hypotympanic fossa to the "true" tympanic cavity. It seems unlikely that such a wide open connecting air space could produce the masslike behavior suggested by this terminology.

In summary, *Tarsius* and anthropoids show general similarities in the internal carotid artery pathway and the organization of the middle ear spaces and septa. However, significant differences in structure are subsumed under the terms "perbullar" (Cartmill, MacPhee, and Simons, 1981) and dual cavity-septum configuration. Since marked differences are present in the construction of the foramen passage (anterior aditus), and this feature is central to the evolution of the middle ear form-function complex, we interpret the similarities as convergent anatomical correlates of middle ear function. Also, *Tarsius* lacks the mastoid air cells characteristic of anthropoids. As described in the next section, tympanic nerve channels provide comparative anatomical evidence for the convergence theory.

TYMPANIC NERVE CHANNELS

The tympanic nerve (of Jacobson) typically leaves the glossopharyngeal nerve (IX) at the level of the inferior ganglion. The posterior carotid foramen or a separate tympanic canaliculus may transmit the nerve into the tympanic cavity in the vicinity of the fenestra cochleae. On the promontory, the tympanic nerve joins the caroticotympanic (sympathetic) nerve fibers to form the tympanic plexus. The tympanic plexus gives branches to the middle ear mucosa, and some fibers exit the middle ear as the lesser petrosal nerve. It is well known that nerves tend to maintain their anatomical relationships with associated structures despite other morphological changes during evolution. In this way, tympanic nerve pathways can be used as "datum

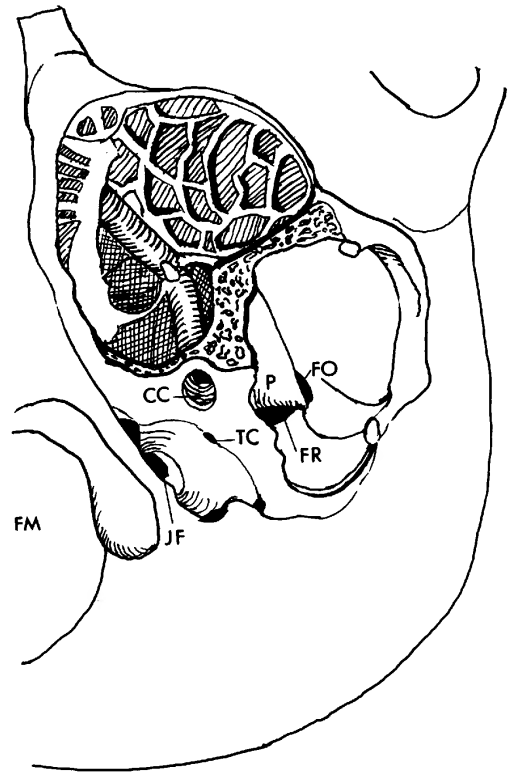


FIG. 3. Ear region of *Cebuella pygmaea*, pygmy marmoset, with bulla open. Note trabecular anterior accessory cavity. Subvertical orientation of carotid canal is reminiscent of condition in *Tarsius* (see text).

points" for comparing the morphological transformations of the internal carotid artery pathways in *Tarsius* and anthropoids.

A tympanic canaliculus in the bridge of bone (petrosal) between the jugular foramen and the carotid foramen transmits a major branch of the tympanic nerve into the tympanic cavity in all living haplorhines except *Tarsius*. In three cadavers of *Tarsius syrichta*, the tympanic nerve passed into the tympanic cavity via a narrow aperture situated between the petrosal bulla and an overlapping lamina of the occipital bone. This aperture could be seen posterior to the jugular foramen in skulls of all species of *Tarsius*, including the montane variety from Sulawesi, although there was some variation in its conformation. Figure 4 shows the tympanic nerve as it enters the aperture, reappears at the pos-

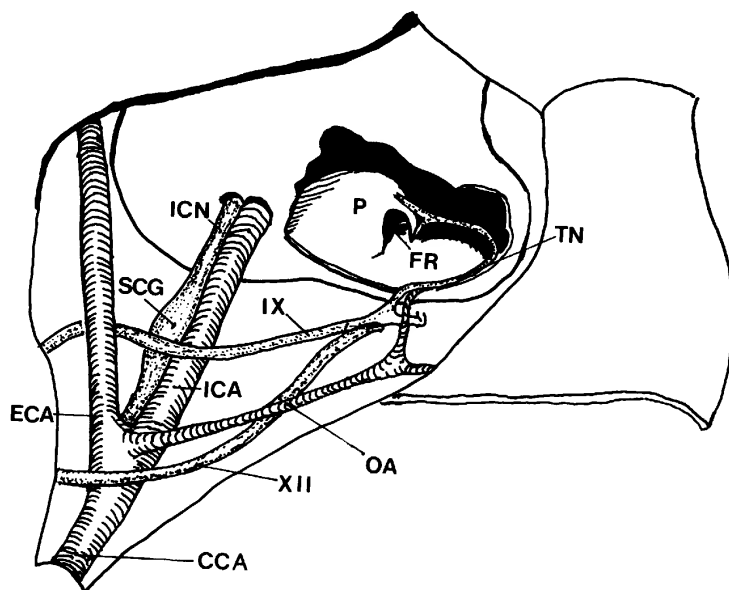


FIG. 4. Tympanic nerve in *Tarsius syrichta*. Nerve enters an aperture between petrosal bulla and a lamina of occipital bone overlapping medial base of bulla. It passes into posterior part of tympanic cavity and reaches the promontory close to fenestra cochleae as in other mammals. Nerve has been lifted off bulla floor so that its course can be clearly seen.

teromedial corner of the tympanic cavity, and from there passes directly to the promontory.

Although this tympanic nerve channel appears to be unique in primates, the nerve enters the tympanic cavity beneath the fenestra cochleae as in anthropoids and mammals generally. In this respect, tympanic nerve pathways are phylogenetically conservative in comparison with the routing of the internal carotid artery. We could not find any tympanic nerve fibers passing through the anterolaterally-shifted carotid foramen in *Tarsius*.

In contrast, at least one branch of the tympanic nerve passes through the carotid foramen in tupaiids and in at least some nonlorisiform primates (MacPhee, 1981; this study). This is true of the adult specimen of *Tupaia glis* we dissected. However, MacPhee (1981) described a second tympanic nerve branch in fetal *Tupaia glis* which passed through a foramen situated at the original site of fusion between the petrosal and entotympanic elements of the tupaiid tympanic floor. This foramen appears to be a variable feature of adult tupaiid skulls (see fig. 6). In the wool-

ly monkey *Lagothrix lagotricha* (AMNH 74422), two subequal branches of the tympanic nerve left the inferior ganglion. One branch followed the internal carotid artery into the carotid canal and the second branch passed through a small tympanic canaliculus situated adjacent to the carotid foramen. Some skulls of *Lagothrix* (e.g., AMNH 74423) had virtually identical foramina, whereas others (e.g., AMNH 74422) displayed a larger tympanic canaliculus situated more posterior in proximity to the mastoid canaliculus.

In *Rooneyia viejaensis*, the carotid foramen and the jugular foramen are separated by a narrow bridge of bone as in *Lagothrix* and *Tupaia*. We were unable to locate a separate tympanic canaliculus either on the external or intratympanic surfaces of the fossil petrosal. Since the presence of a separate tympanic canaliculus in lemuroids is correlated with the absolute distance between the carotid foramen and the jugular foramen (table 1), it is probable that at least a part of the tympanic nerve passed through the carotid foramen in *Rooneyia*.

In at least some anthropoids, therefore, a

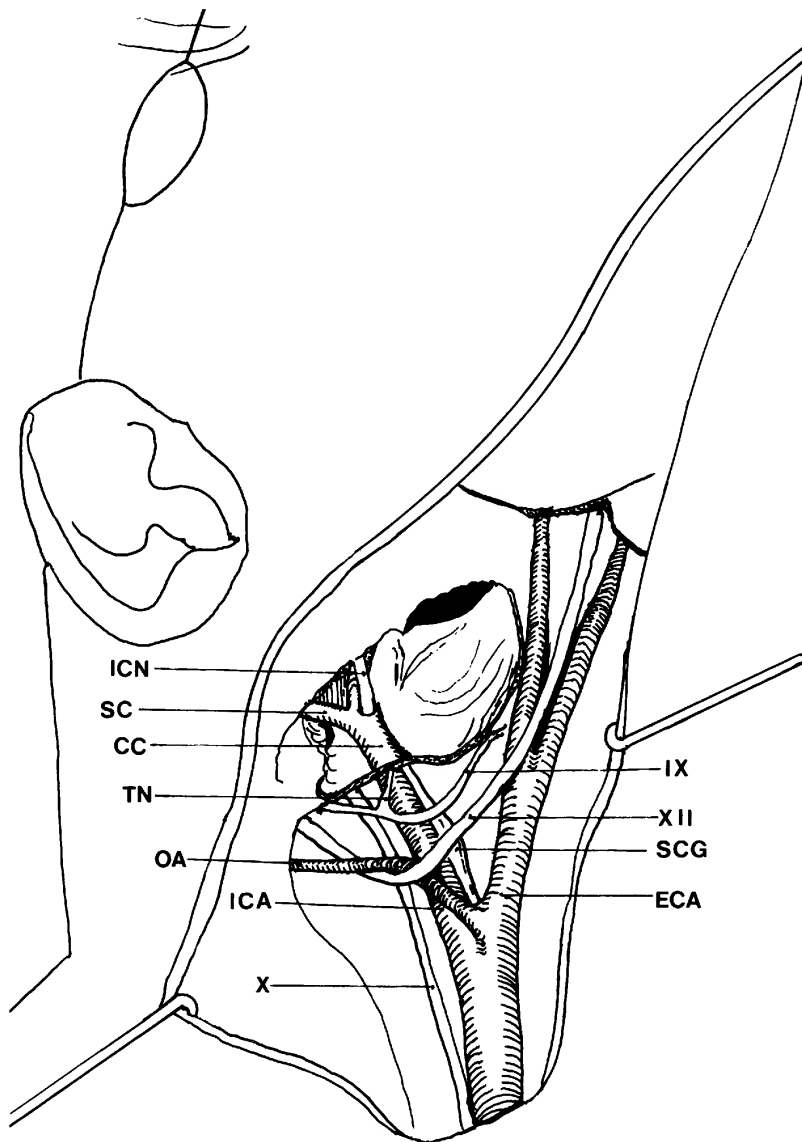


FIG. 5. Tympanic nerve in *Tupaia glis*. A nerve branch follows internal carotid artery and nerve into carotid canal and reaches promontory close to the fenestra cochleae.

branch of the tympanic nerve follows the internal carotid artery into the carotid foramen, whereas no fibers could be found crossing the bulla in order to reach the carotid foramen in *Tarsius*. It can be concluded that the anthropoid internal carotid entry point is more primitive, i.e., tupaiid or omomyid-like, than the specialized anterolateral position in *Tarsius*. The carotid shift is greater in *Tarsius* despite the fact that *Lagothrix* is a much larg-

er animal. Thus, the differences in the internal carotid artery pathways of *Tarsius* and anthropoids are not just a matter of degree, but affect the morphological relations of associated structures.

A tympanic canaliculus in the bridge of bone between the jugular foramen and the carotid foramen is a shared character of all Anthropoidea (e.g., *Cebuella*, fig. 3). If the original carotid shift in an ancestral tarsier

TABLE 1
Presence of the Tympanic Canaliculus in Some
Lemuroidea

<i>Lepilemur</i> (6)	Absent
<i>Haplemur</i> (5)	Absent
<i>Avahi</i> (4)	Absent
<i>Lemur</i> (19)	Variable
<i>Varecia</i> (7)	Present
<i>Propithecus</i> (6)	Present
<i>Indri</i> (5)	Present (in association with a bony tube)

Number of specimens of each genus in parentheses.
Genera are listed in order of increasing body size.

was accompanied by the establishment of a new tympanic nerve channel in the occipital-petrosal aperture, then it was probably an event that occurred following the *Tarsius*-anthropoid divergence.

INTERNAL CAROTID NERVE CHANNELS AND ARTERIAL CANAL MEASUREMENTS

The cephalic arterial pattern of fossil species is inferred from the diameters of bony canals for the promontorial and stapedia branches of the internal carotid artery (Gingerich, 1973; Szalay, 1975a). These canals may be open channels on the promontory or complete bony tubes in the middle ear. Szalay (1975a) proposed that a promontorial artery larger than the stapedia artery was a derived character linking omomyids with living haplorhines and distinguishing them from contemporary adapids. On the other hand, Gingerich (1973) and Gingerich and Martin (1981) have shown that some adapids have relatively large bony tubes for the promontorial artery. However, both of these positions can be questioned because the presence of an arterial canal does not always imply the presence of a corresponding artery (Conroy and Wible, 1978). In at least some *Varecia variegata* (Conroy and Wible, 1978) and *Lemur catta* (Bugge, 1974), the promontorial artery is obliterated distal to the origin of the stapedia artery, so that the internal carotid nerve is the sole occupant of the open "vascular" channel. The internal carotid nerve is the major postsynaptic sympathetic trunk proximal to the superior cervical ganglion. It supplies sympa-

thetic innervation to visceral structures of the head and neck. These findings created considerable uncertainty about the validity of arterial canal measurements. So uncertain was the situation that Gingerich and Martin (1981) were led to assert that the systematic interpretation of fossils should be based on the relative sizes of the *canals* rather than the arteries. The results of this approach can be misleading. For example, some indriids have separate channels on the promontory for the promontorial artery and the internal carotid nerve which, if confluent, would give the misleading impression of a relatively large artery.

Nevertheless, there is strong reason to expect that a large artery and nerve trunk would not occupy the same bony tube. It is well known that nerves react adversely to compression. For example, Rizzo, Bosch, and Gross (1982) assigned part of the cause of a trigeminal neuropathy to the pulsation of a dilated middle meningeal artery, which had eroded the foramen spinosum until it became continuous with the foramen ovale. Bony tubes encapsulate(d) the internal carotid (promontorial) arteries of tupaiids, tarsoids, and some Eocene lemuroids. It is probably due to the potential for nerve compression that, in tupaiids, the main trunk of the internal carotid nerve does not remain in the arterial canals. The nerve trunk emerges through a foramen in the distal end of the funnel-shaped carotid canal (cf. MacPhee, 1981). Through its initial course in the carotid canal, the nerve sends numerous offshoots to supply the artery. The nerve subsequently travels in a spiral groove on the *external* surface of the bony canal for the large promontorial artery. Some skulls of *Tupaia glis*, particularly those of *T. g. modesta* (e.g., AMNH 59581), showed a divided carotid foramen and a separate bony tube for the nerve trunk alongside the carotid canal (fig. 6). This tube opened onto the carotid canal at the precise point occupied by the nerve foramen in other tupaiid skulls.

Tarsius also has separate foramina and bony tubes for the large internal carotid artery and nerve trunk (fig. 1). The foramen and tube for the internal carotid nerve is the one misidentified by Saban (1963) as the "canal of Jacobson" for the tympanic nerve.

The middle ear carotids of *Rooneyia vie-*

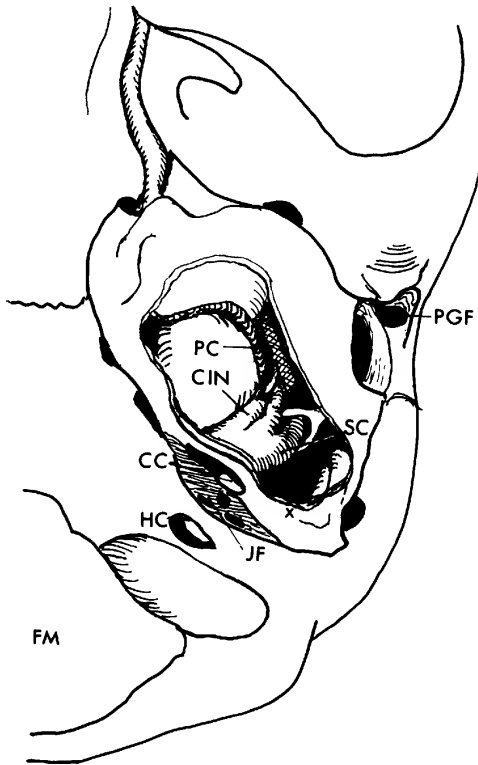


FIG. 6. Skull of *Tupaia glis* based on AMNH 59851 showing a separate bony tube for internal carotid nerve. X marks the spot where a separate foramen for tympanic nerve is variably found in tupaiid skulls.

jaensis were enclosed in bony tubes (fig. 7). Two foramina could be identified along the bony tubes. The first was situated near the proximal end of the carotid canal and the second in the promontorial canal just distal to the bifurcation (fig. 7). We suspect that the foramen in the carotid canal is an artifact caused by matrix breaking through the canal. However, there is no doubt that an actual foramen is present in the promontorial canal since a spiral groove could be seen emanating from it. This latter arrangement closely resembles the morphology in *Tupaia*. The foramen probably transmitted nerve fibers out of the arterial canal in order to avoid compression from artery pulsations. It is very likely, therefore, that the promontorial artery in *Rooneyia* was large and filled its canal almost completely as in *Tupaia*. The high

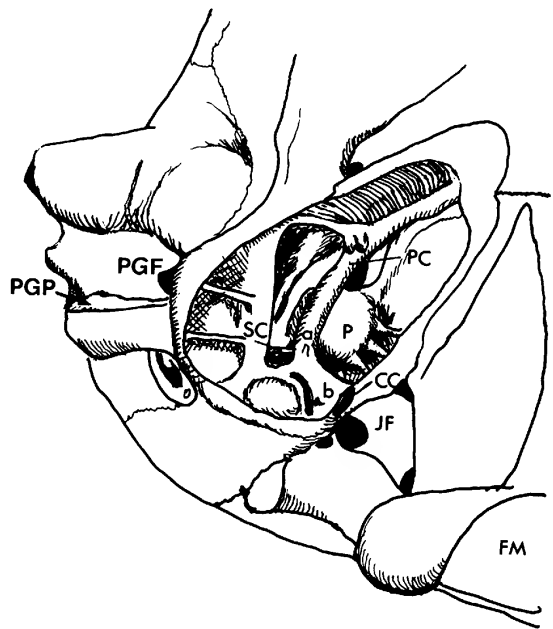


FIG. 7. Middle ear of *Rooneyia viejaensis* showing where internal carotid nerve may have emerged from bony arterial canal. Note transpromontorial pathway of internal carotid artery and the postglenoid process appressed and fused to the bony meatal tube (modified from Szalay, 1976).

probability that the size of the promontorial artery in *Rooneyia* is accurately represented by its bony tube supports Szalay's (1975a) hypothesis (see above), although there is a smaller size difference between the promontorial and stapedial canals in the European omomyid *Necrolemur* (Szalay, 1975a).

Unlike that in modern lemuroids, a complete bony tube for the promontorial artery as it crosses the promontory is present in a number of Eocene adapids. Gingerich (1973) has shown that a skull of *Notharctus tenebrosus* (AMNH 11466) has a promontorial canal larger than the stapedial canal and Gingerich and Martin (1981) have described a skull of *Adapis parisiensis* with bony tubes of similar proportions. We examined complete arterial canals in the adapids *Notharctus*, *Adapis magnus*, *Smilodectes gracilis*, and *Mahgarita stevensi*, but were unable to identify an internal carotid nerve foramen or spi-

ral groove. In *Adapis magnus* the promontorial canal became an open channel distal to the promontory. In *Smilodectes* the canals were complete but partially covered with matrix, whereas in *Mahgarita* they were not sufficiently well preserved. The situation in *Notharctus* is surprising considering that no visible exit for the internal carotid nerve could be found along the well-preserved arterial canals despite the fact that some fibers must have left the bony tube as the caroticotympanic nerve. In the groove between the promontorial (carotid) canal and the promontory close to where the caroticotympanic nerve is given off in platyrrhines, there is still some unremoved matrix. If there is a foramen in this location, then it might indicate that the internal carotid nerve was plexiform in *Notharctus* as in anthropoids (see below). On the other hand, if the absence of a *Tupaia*-like arrangement indicates that the promontorial artery was much smaller than its canal, then the presence of a complete bony tube is unexpected.

Pulsations of the internal carotid (promontorial) and stapedia arteries produce volume and pressure variations in the tympanic cavity which influence hearing in some mammals (Packer, 1983, ms). Calculations have shown that the arterial sound spectrum in the tympanic cavity is close to low frequency thresholds of hearing in *Tupaia glis*, indicating that the threshold values are adapted to the noise. Fleischer (1978) was correct in suggesting that the bony canals act as noise attenuating structures. The completeness of the carotid (promontorial) canal is directly related to artery (or canal lumen) size in living and fossil primates, which is to be expected since pulsations are scaled to the size of the vessel. If the noise attenuation hypothesis is correct, then the complete promontorial tube indicates that a relatively large promontorial artery was present in *Notharctus* (AMNH 11466). Needless to say, internal carotid nerves do not pulsate and need not be enclosed for this reason, although in primates a complete canal usually forms around the facial nerve. In Eocene lemuroids the fairly wide distribution of complete promontorial canals suggests that a large promontorial artery is either primitive for

lemuriforms (and thus euprimates generally) or a condition that evolved several times in early lemuroids.

The carotid canals of *Aotus* and *Lagothrix* were dissected to further test the nerve compression hypothesis. In the carotid canals of these two platyrrhines, the internal carotid nerve is approximately intermediate in form between the largely coherent trunk seen in prosimians and the fine meshwork (plexus) seen in man. One *Aotus* showed a bony partition between the internal carotid artery and the largest fiber bundle. One skull of *Cebuella pygmaea* was found that closely resembled *Tarsius* in having separate foramina and bony tubes for the artery and nerve running along the transverse septum. (We have already remarked on the resemblances between the smallest platyrrhines and *Tarsius*.) A single *Alouatta* skull, among the 30 examined, showed a carotid canal divided by a bony partition. A plexiform nerve is presumably less susceptible to compression in part because of the venous plexus surrounding the artery.

In summary, the size of the promontorial artery in *Rooneyia* is probably accurately represented by the internal diameter of the relatively large bony tube. The use of this feature as a synapomorphy of an omomyid-*Tarsius*-anthropoid clade (Szalay, 1975a) is based upon the assumption that a large promontorial artery was not also characteristic of other Eocene prosimians (e.g., a primitive euprimate condition). There is some inconclusive evidence both for and against this assumption (see also Conclusions).

THE BONY MEATAL TUBE

The external auditory meatus is an air-filled tube which extends from the concha to the tympanic membrane. The meatal tube protects the tympanic membrane and middle ear from injury and provides a frequency-dependent sound pressure transformation from the free field to the tympanic membrane (Shaw, 1974). The meatus has a medial bony part and a lateral cartilaginous part continuous with the pinna. In human neonates and various adult mammals, the bony part is represented only by the incomplete ring of bone

holding the tympanic membrane, the ectotympanic, together with the temporal bone that completes it dorsally. In extant adult catarrhines including man, the bony meatus comprises a tubular expansion of the ectotympanic bone completed dorsally by a squamous temporal roof. Tubular bony meatal structures in other mammals are usually formed by the ectotympanic, but in some cases by other skeletal components of the tympanic floor or adjacent parts of the temporal bone (see van der Klaauw, 1931). Meatal morphology is heavily weighted in primate systematics and phylogenetic studies even though there remain significant unsolved questions concerning the functional significance and homologies of bony meatal structures (cf. Rosenberger and Szalay, 1980). It is the purpose of this section to propose a functional explanation for bony meatal structures in mammals, and to discuss its implications for the systematic interpretation of meatal morphology in primates.

The meatal walls, when vibrating in response to the application of a vibrator to the skull or mandible, radiate sound energy into the ear canal lumen. Experiments performed by Békesy (1960) have shown that the radiation of bone-conducted sounds into the human ear canal is increased by vibratory motions of the mandible. In man, the anterior wall of the meatus forms the posterior, non-articular wall of the jaw joint. Some portion of the sound energy in the ear canal is generated by direct contact between the condylar process of the mandible and the anterior meatal wall. When the mandible was shifted laterally so that the condyle came to border on the cartilaginous portion of the meatus, a sharp increase in the loudness of the bone-conducted tones was heard. Displacements of the easily movable cartilaginous portion of the meatus increased the amplitude of volume and pressure changes in the ear canal picked up by the tympanic membrane (Békesy, 1960).

Human morphology contrasts with that of the domestic cat (*Felis catus*) where a broad postglenoid process of the temporal bone completely separates the glenoid fossa (jaw joint) from the cartilaginous meatus. Accordingly, Tonndorf, Greenfield, and Kauf-

man (1966) reported no appreciable difference in bone conduction responses registered by the cochlear microphonic before and after mandibular resection in cats.

Although signals of known magnitude and frequency were used in the bone conduction experiments involving human subjects, chewing motions directed against the meatal wall could produce analogous effects. It is possible to hear the disturbing sounds produced by shifting your own mandible laterally against the cartilage and then swinging it back to the rest position. Without the thin but relatively rigid wall of bone (bony meatal tube) directly behind the jaw joint, the radiating surface for sound would be greatly increased. In other mammals with a similar structural relation between the jaw joint and the external ear, such disturbing sounds (noise) would mask important, relevant auditory signals, and the ability of animals to retain near normal hearing acuity while chewing is clearly of considerable survival value. This is especially true among herbivorous mammals in which both the large intake and the lengthy processing of foodstuffs keep the masticatory apparatus in continual use.

On the basis of the bone conduction experiments, then, a tubular bony meatus is expected in those species where the jaw joint borders directly on the external ear. Among the living higher primates, all juvenile catarrhines and adults of the small-bodied forms resemble *Homo* in having the jaw joint bordering directly on the meatus. With the progress of basicranial remodeling in large-bodied, non-hominid catarrhines (Ponginae, *Papio*), however, this close structural relation is normally lost.

Primitively, as in felids, lemuriforms, platyrrhines, and some lorisooids, the bony meatus is limited to a ringlike ectotympanic. In all these forms the postglenoid process of the temporal bone intervenes between the jaw joint and the cartilaginous meatus. Exceptionally long and stout postglenoid processes are found in *Alouatta*, Indridae, the giant subfossil lemur *Megaladapis*, as well as the koala *Phascolarctos*, which can be correlated with the mandibular mobility and constant chewing stresses incurred by leaf-eaters. The

bony portion of the meatus in *Megaladapis* (Saban, 1963, 1975) is mainly "intrabullar" extending only slightly laterally beyond the tympanic cavity (see below). The large postglenoid process probably served to protect both the postglenoid vein and the cartilaginous meatus from motions of the apparently broad mandibular condyle. The edentate leaf-eater *Bradypus infuscatus* (three-toed sloth), by comparison, has a jaw joint bordering directly on the bony bulla (cf. *Phaner furcifer*, below). A so-called false external auditory meatus is formed in some lorises in which expanded postglenoid and zygomatic processes of the temporal bone form the anterior wall and the posterior root of the zygoma and the squamous temporal bone form a broad roof continuous with the mastoid (cf. van der Klaauw, 1931; Simons, 1961). In *Arctocebus*, the bulla (petrosal) shows a cylindrical lengthening which forms a short bony floor. The jaw joint borders directly on this bony "meatus spurium."

Craniofacial specializations that cause a crowding of structures in the infratemporal region, resulting in a jaw joint that borders directly on the external meatus, must be several and varied. Small body size, the degree of cranial kyphosis, the position of the foramen magnum which in turn may be related to posture or encephalization, the relative proportions of the cranial and mandibular attachments for the muscles of mastication, and auditory specializations are certainly some of the interrelated factors. For present purposes, the essential point is that a bony meatal flange or a well-developed bony tube is produced in species where the jaw joint borders directly on the external ear. Furthermore, we have found a good correlation between the width of the mandibular condyle and the length of the osseous portion of the meatus.

In *Tarsius* (fig. 9) and the Paleogene omomyid tarsoids *Rooneyia*, *Necrolemur*, and *Tetonius* (reconstructed skull, Szalay, 1976), the jaw joint borders on the bony meatal tube as in man. The postglenoid process is vestigial in all these tarsoids. In *Rooneyia* it is reduced to a thin plate of bone appressed and fused to the meatal tube (fig. 7), whereas in *Tarsius* it is further reduced to a nodule or spicule of bone (fig. 9). Since the usual space

between the postglenoid process and the external meatus is obliterated in these tarsoids, the large postglenoid foramen for the postglenoid vein is situated anteromedial, rather than posterior, to the postglenoid process.

Very similar functional morphology is characteristic of the Australian marsupials *Petaurus* (fig. 8) and *Pseudocheirus* (Petauridae) and *Phalangista vulpina* (Phalangeridae). The condylar processes in *Petaurus* and *Pseudocheirus* are intimately related to the bony meatal tube. In the Victorian ring-tailed possum *Pseudocheirus peregrinus* the squamous temporal bone (postglenoid process) and the ectotympanic form equal dorsal and ventral halves, respectively, of the meatal tube. A comparable "postglenoid temporal arch" is integrated into the long bony meatus of the subfossil lemuroid *Archaeoindris*. The burramyid marsupial *Cercartetus concinnus* has a short ectotympanic tube in direct association with a narrow mandibular condyle.

In the elephant shrew *Elephantulus* (Macroscelididae), the ectotympanic is expanded to form the anterior coronal half of a bony meatal tube. The posterior half of the meatus remains cartilaginous since it does not participate in the wall behind the jaw joint. The postglenoid process is vestigial. The bony meatus is relatively more complete posteriorly in *Rhynchocyon*.

Still another example of this relationship is found in the six-banded armadillo *Euphractus sexcinctus*. In this species, the jaw joint borders directly on the long bony tube, which is complete except for a small gap in the ventral wall.

Smaller contributions of bone to the external meatus are found in some species not usually described as possessing an osseous portion. In at least some *Aotus trivirgatus*, the anterior crus of the ectotympanic ring is slightly broadened or flanged and approaches the laterally-situated postglenoid process, thereby forming a more or less complete bony wall behind the jaw joint. Also, the postglenoid foramen of *Aotus* resembles that of tarsoids in its position anteromedial, rather than posterior, to the postglenoid process. Callitrichids show a long, dorsoventrally narrow extension of the anterior crus of the ectotympanic which participates in the wall behind the jaw joint. The remainder of the ring is

unexpanded. In *Tupaia glis*, the entotympanic bone (bullae) overlaps the "free" intrabullar tympanic ring to produce a lateral meatal flange. This bony flange is very pronounced in the tupaiid *Lyonogale tana* where it extends laterally beneath the postglenoid process (fig. 9). Among cheirogaleids, *Microcebus* skulls often show a slight tubular expansion of an overlapping petrosal bone (bullae). In *Phaner*, the mandible abuts against the postglenoid process, which in turn is appressed against a slightly expanded meatal rim of the bulla. Any entectal movements of the mandible would bring the condyle into contact with the flattened and thickened anterolateral corner of the bulla.

When the mandible and skull of the Norway rat (*Rattus norvegicus*) are articulated, the structural relation between the jaw joint and the external meatus appears to be relatively remote. This is despite the absence of a postglenoid process of the temporal bone. However, during the preparatory stroke of mastication the mandible is shifted backward about 1.5 mm. beyond the point at which the first upper and lower molars are opposite each other (Hiimae and Ardran, 1968). Although these authors did not comment on it, mandibular retraction apparently causes the condyle to ride against a flattened area of the auditory bulla until it reaches the flared anterior meatal rim of the bulla. The remainder of the meatus is cartilaginous. The same morphology is seen in *Sciurus*. If such propalinal movements are also performed by beavers (*Castor*), then the mandibular condyle should be brought into contact with the beaver's well-developed bony meatal tube. The same explanation appears to pertain to bony meatal structures in other rodents.

The cineradiographic study of Ardran, Kemp, and Ride (1958) demonstrated that propalinal movements in rabbit mastication are quite limited. Mandibular retraction did not proceed beyond a rest position where the first upper and lower molars are opposite each other. It appears doubtful, therefore, that the condylar process of the mandible would contact the bony meatal tube of the rabbit anytime during the chewing cycle. On the other hand, it is possible that the large masseter muscle may bulge against the bony meatus.

The striped skunk *Mephitis* and the rac-

coon *Procyon* also do not fit clearly into this framework since adult skulls combine a bony meatal tube with a large postglenoid process. The long meatal tubes in these species are tucked well underneath the skull so that the styloid, pharyngeal, and/or masticatory musculature may have influenced meatal elongation. The situation in *Canis* provides some evidence for this effect. In dogs, the slender stylohyoid muscle runs along a flange-like extension of the posterior meatal rim (Miller, 1964). Upon contraction this muscle would bulge against the bony flange. Muscle contractions produce a broad band noise with a center frequency of about 400 Hz (McKusick, 1958). The rigid bony flange should reduce the level of these muscle sounds radiated into the ear canal. If this hypothesis is correct, then it is not difficult to see how much larger muscles, such as the posterior belly of the digastric, could favor the evolution of a bony meatal tube. The origin of the stylohyoid muscle ventral to the meatus in cats probably accounts for the absence of the posterior meatal flange in these forms.

In most mammals, the original membranous floor of the tympanic cavity is functionally replaced by a rigid bulla. According to Fleischer (1978) and MacPhee (1981), the chief function of the bulla may be to prevent deformation of the tympanic cavity caused by contraction of the masticatory muscles, particularly the posterior belly of the digastric. These authors suggested that such deformation or compression would increase the stiffness of the middle ear cavity and thus affect low frequency hearing. Additionally, the muscle contractions could radiate disturbing noises into the tympanic cavity from its walls.

Because of the relatively remote structural relation between the jaw joint and the external ear in large, specialized ungulates such as *Equus* and *Ovibos*, their bony meatal tubes appear to be redundant from the standpoint of "chewing" noises set up in the ear canal. Moreover, there is a broad "gap" between the postglenoid process and the bony meatal tube in *Equus* skulls which further isolates the external ear from the jaw articulation. This anatomical arrangement may be an adaptation to the large size of the chewing forces that must be dissipated. Forces exerted on

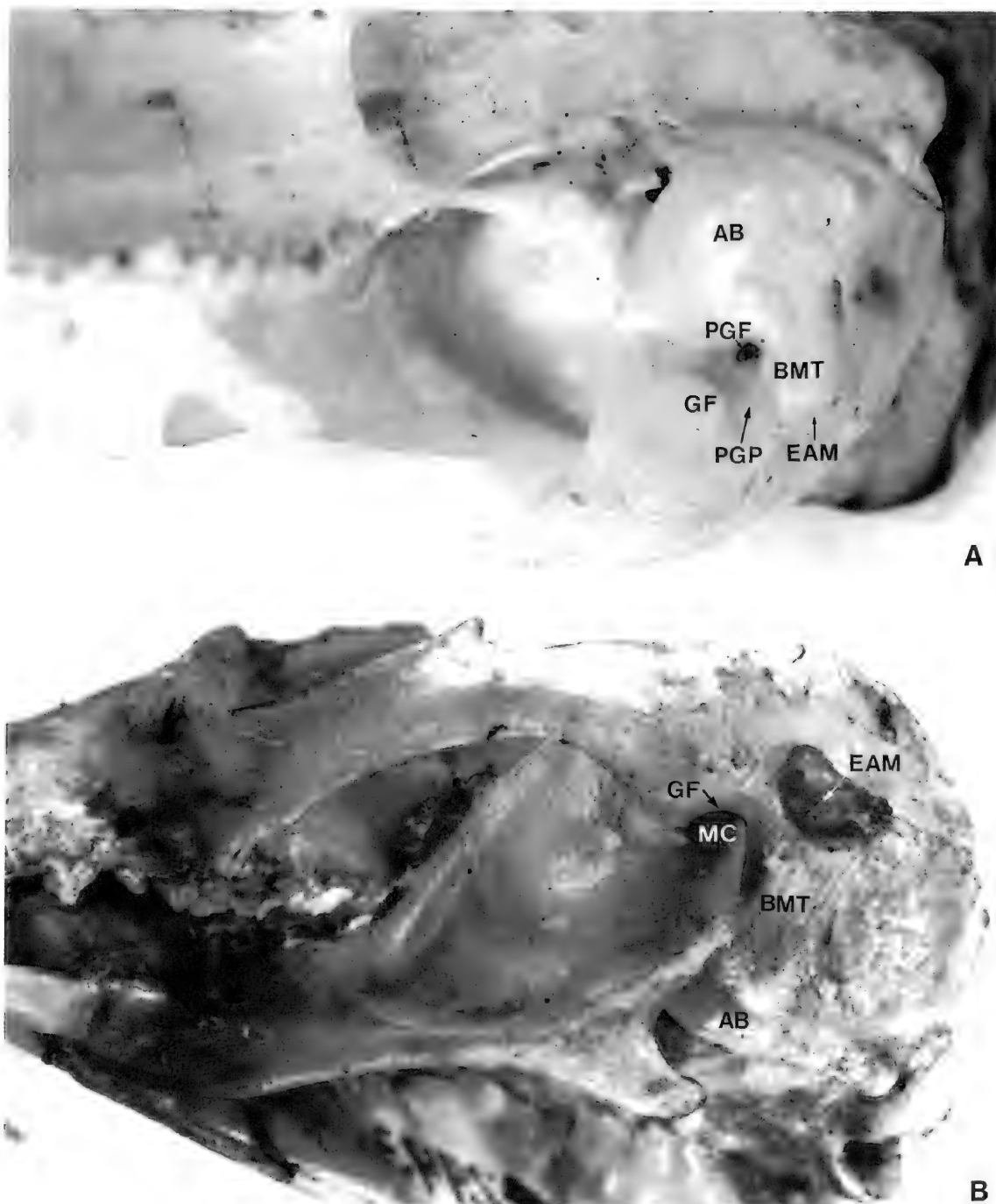


FIG. 8. Photographs illustrating direct structural relation between jaw joint (mandibular condyle) and bony meatal structures in (A) *Petaurus breviceps* and (B) *Petaurus* with mandible articulated.



FIG. 9. Photographs illustrating direct structural relation between jaw joint and (A) bony meatal flange in *Lyonogale tana* and (B) bony meatal tube in *Tarsius* sp. (B) is adapted from Szalay (1976) and shows position of mandible in relation to bony meatal tube at onset of power stroke. Note also clinocranial type of skull.

the bone by muscle contractions may also be important. Nevertheless, the long bony external meatus of the "primitive" artiodactyl *Tragulus javanicus* (the mouse deer) forms a bony wall directly behind the jaw joint in the expected manner.

In summary, the bony meatal tube is an adaptation designed to reduce physiological noise produced by motions of the mandible during mastication in species where the jaw joint borders directly on the external ear. The wall of bone is thin but relatively much more rigid than the easily movable cartilage. The latter would act as a radiating surface for disturbing sounds capable of masking important, relevant auditory signals. In other species, there is enough room in the infratemporal region for the imposition of a postglenoid process of the temporal bone between the jaw joint and the cartilaginous meatus. In primates, the structural relation between the jaw joint and the meatus may be dependent on body size, the degree of facial and/or basicranial flexion, the position of the foramen magnum, specializations of the masticatory apparatus (compare early Tertiary *Plesiadapis* and *Phenacolemur* with diprotodont marsupials), auditory specializations (e.g., bulla expansion), or most likely a total morphological pattern of the skull influenced by several of these factors. Since none of these causal features is an indicator of phylogenetic affinities *per se*, the bony meatal tube must also be considered a weak indicator of affinities (i.e., it is subject to convergence). However, this does not mean that forms characterized by a bony meatal tube can easily evolve into forms lacking it or vice versa, as implied by Cartmill, MacPhee, and Simons (1981) who described the bony meatal tube as "highly labile." The most interesting conclusion we derive from the functional analysis of bony meatal structures is that the production of a bony tube in euprimates can be correlated with the tarsiod "type" of skull (*sensu* Le Gros Clark, 1960). In *Tarsius* and to a varying extent in the fossil tarsiods, the cranium is compressed rostrooccipitally. The anterior parts of the basicranium are narrowed in a rostral direction, thus bringing the back of the palatal complex (pterygoid, palatine, and maxilla) into relatively close relation to the ear. The compression of the an-

terior basicranial elements is related to the rostral elevation of the brain (cranial kyphosis), which Hofer (1952) described as clinocrany (see fig. 9). Therefore, it is difficult to conceive of a *Tarsius* type skull without a close structural relation between the jaw joint and the external ear. This argument apparently holds for the rounded crania of omomyids, although the basal axis of the skull is straighter in these forms. This is despite the fact that a hypothetical tarsiod ancestor of Anthrozoidea, whether tarsiid or omomyid, cannot possess a bony meatal tube since it is absent in New World anthropoids and the oldest known Old World anthropoids (Gingerich, 1973; Hershkovitz, 1974). Meatal morphology is a sound reason for thinking that the skull at the earliest stages of anthropoid evolution resembled the skulls of generalized adapids such as *Mahgarita*, *Notharctus*, or *Pronycticebus* more than the tarsiod (particularly *Tarsius*) type of skull. It is a moot question whether such a form would be recognized as tarsiod or lemuroid since we do not know how the skull of a relatively large, apparently folivorous tarsiod such as *Macrotarsius* might have differed from those of *Mahgarita* or *Notharctus* (see also Conclusions).

Homologies of bony meatal tubes can be assessed by skeletal composition and the ectotympanic-petrosal plate relationship. If the latter criterion is used, then the bony tubes in omomyids and *Tarsius* would be parallel specializations, whereas the bony tubes in omomyids and plesiadapoids would appear to be homologous. Gingerich (1976) used this feature in support of his conception of "Plesitarsiiformes," although this idea was recently abandoned by him (see MacPhee, Cartmill, and Gingerich, 1983). The bony meatal tubes in the fossil taxa have an "intrabullar" (aphaneric) portion consisting of an ossified annular bridge between the tympanic ring and the meatal rim of the bulla. However, no sutures are visible so that the annular bridge could be an expanded ectotympanic, an inwardly expanded linea semicircularis of the petrosal bone (MacPhee, 1977; Conroy, 1980), or an independent ossification. Furthermore, the intrabullar position of the original ring holding the tympanic membrane in omomyids and plesiadapoids is apparently a primitive

primate condition providing no evidence of special affinity (e.g., Le Gros Clark, 1960).

The occurrence of meatal elongation in *Lyonogale tana* and *Allocebus trichotis* (Cartmill, 1975) in conjunction with an intrabullar tympanic ring and an anulus membrane indicates that the ossified anular bridge has a function independent of the extrabullar portion of the bony meatal tube. The anulus membrane of tupaiids and lemuriforms may act as an admittance in parallel with the tympanic membrane admittance. In this respect, its shunting effect would be qualitatively similar to that portion of the tympanic membrane not coupled to malleus motion (see Tonndorf and Khanna, 1972; Lynch, 1981). The stiffness and relatively small surface area of the anulus membrane in living tree shrews and lemurs indicates that the shunting effect is small. However, the shunting effect of a broader anulus membrane could have been large enough to favor ossification, as for example in *Rooneyia*, *Plesiadapis*, and *Megadadapis*. The shunt can also be closed by fusing the ectotympanic ring directly to the bulla wall as in *Tarsius* and anthropoids.

CONCLUSIONS

The hypothesis of Cartmill and Kay (1978) that *Tarsius* is the closest known relative of Anthropoidea was based on an interesting reappraisal of haplorhine middle ear morphology. Particular weight was placed on the intrapetrosal route and relations of the internal carotid artery and the arrangement of the principal spaces and septa of the middle ear. Their character analyses were later summarized by Cartmill, MacPhee, and Simons (1981) whose use of the term "perbullar" to describe the internal carotid artery pathway in *Tarsius* and anthropoids also reflected the dual cavity-septum arrangement of the middle ear. These morphological traits were considered to be shared derived characters of *Tarsius* and anthropoids, and defining characters of Haplorhini, whereas omomyids were regarded as primitive euprimates having no demonstrable relationship with living haplorhines. Through the use of tympanic nerve channels, we have shown that the anterolateral shift of the carotid foramen and its con-

tents in *Tarsius* is not characteristic of anthropoids. Thus, different morphological transformations seem to be the origin of observable differences in the internal carotid route and relations. The dual cavity-septum configurations of *Tarsius* and a typical platyrrhine *Saimiri* have similar acoustics despite marked differences in the construction of the foramen passage (anterior aditus), and the *Tarsius* middle ear lacks the mastoid cells characteristic of anthropoids. In addition, the bony meatal tube is characteristic of the tarsier type of skull but absent in primitive anthropoids. For these reasons, we have interpreted the undoubted morphological similarities between *Tarsius* and anthropoid auditory regions as convergent specializations. It is a moot question whether the last common ancestor of *Tarsius* and Anthropoidea resembled known Paleogene prosimians or whether it showed some advance toward the vertical placement of the carotid canal, obliteration of the stapedial artery, increased pneumatization in the apical area of the bulla, and elimination of the anular bridge. The auditory region and skull in the *Tarsius* lineage appears to be too specialized to have been transformed into the type characteristic of platyrrhines (cf. Rosenberger and Szalay, 1980). On the other hand, a last common ancestor of *Tarsius* and anthropoids in which the auditory region resembled those of cebids such as *Saimiri* or *Aotus* is certainly a possibility.

Szalay and Delson (1979) considered certain features of the skull which may distinguish tarsiods and anthropoids from lemuroids. However, several of the craniodental features traditionally used to distinguish omomyids from adapids are size-dependent. For example, the retention of four premolars in large adapines but not in *Mahgarita* or any omomyids is probably a function of tooth crowding in small, short-snouted animals. Among non-primates, *Martes* has one more premolar than *Mustela* despite the closely similar diets. The specialized molars of the large adapids were clearly adapted to leaf-eating, a diet which is inefficient for small animals. It is probably for this reason that the small adapids *Anchomomys*, *Periconodon*, and *Pronycticebus* show a somewhat simpler, omomyid-like, occlusal pattern as-

sociated with an insectivorous/frugivorous diet. Conversely, the relatively large omomyid *Macrotarsius* had molar teeth resembling those of *Alouatta* (Szalay, 1976) and *Notharctus* (AMNH 13025), suggesting that it was a leaf-eater.

A smaller face to neurocranium ratio, a more globular braincase, and greater splanchnoflexure are also size-related features of recognized tarsioids. Even the relatively large promontorial artery of omomyids may be related to small body size. Volume blood flow is proportional to the fourth power of vessel radius according to Pousseuille's formula. Since the transverse foramina of the cervical vertebrae limit the radius of the vertebral arteries, small species may need a second artery to supply the relatively large brain. On the other hand, an increase of only 20% in the radius of the vertebral arteries doubles their capacity to supply blood. It may be for this reason that the promontorial artery is generally most reduced in the large lemuroids *Varecia variegata* and *Adapis magnus* where the vertebral-basilar arteries are the major conduits for blood to the cerebral arterial circle.

The posterolateral position of the posterior carotid foramen is apparently the only specialization of the auditory region in recognized adapids that is not present in anthropoids (Cartmill, MacPhee, and Simons, 1981). It is true that the European adapids are almost identical to modern lemurids in middle ear morphology (cf. *Adapis magnus* and *Varecia*), but the presence of a large promontorial canal in *Notharctus* and *Mahgarita*, the apparent absence of a stapedia canal in *Mahgarita*, and a possible remnant of the stapedia artery in some platyrrhines (fig. 2) show that the carotid arterial pattern does not completely distinguish adapids from anthropoids.

Evidence of placental and fetal membrane morphology (e.g., Luckett, 1975), external characteristics (Pocock, 1918; Jones, 1929), and comparative biochemistry (Goodman, 1975, but see Sarich and Cronin, 1976) indicates that the last common ancestor of anthropoids and prosimians might be described as a tarsioid in the broad sense. However, there may be a problem with using the singular *Tarsius* as a model for tarsioid mor-

phology in general. The latter notion seems to be rooted in T. H. Huxley's conception of the living primates as an "échelle des êtres" in which every major adaptive radiation has a representative living form. Although the cranial morphology associated with a bony meatal tube and a relatively large promontorial artery may be tarsioid characters, the morphological definition of Tarsiodea appears to be too dependent on cranial and dental features related to small size. Therefore, a lemuroid-tarsioid dichotomy for all Paleogene prosimians extending back to the early Eocene is probably a matter of cladistic convenience in theory and size dependent features in practice.

APPENDIX

The frequency of the series resonance of the accessory cavity and the foramen passage (represented as "an intermediate-sized tube") is $f_s = 1/(2\pi)(M_f C_a)^{0.5}$, where M_f is the mass of the air in the foramen and C_a is the acoustic compliance of the accessory cavity. $C_a \approx V/\rho c^2$, where V is the volume of the accessory cavity, ρ is the density of air in g/cc, and c is the speed of sound in cm/s (Lynch, 1981). $M_f = (\rho/\pi \cdot r^2)(L + 1.7r)$, where r is the radius and L is the length of the tube in centimeters. Thus, the frequency of the series resonance depends upon the accessory cavity volume and foramen dimensions.

The frequency of the series and parallel resonances can be roughly estimated from anatomical measurements on *Tarsius* skulls:

Accessory cavity volume ≈ 0.12 cc

Foramen radius ≈ 0.025 cm

Foramen length ≈ 0.08 cm

For the series resonance, $C_a \approx 8 \times 10^{-8}$ cm⁵/dyn and $M_f \approx 8 \times 10^{-2}$ g/cm⁴. Thus, $f_s \approx 2000$ Hz, which is close to the experimentally determined value of $f_s = 2125$ Hz in cat (Lynch, 1981). C_a is roughly an order of magnitude smaller than in cat, while M_f is roughly an order of magnitude larger.

The parallel resonance frequency is given by $f_p = 1/[2\pi(M_f C_{eq})^{0.5}]$, where $C_{eq} = C_a C_t / C_a + C_t$ (Lynch, 1981). C_t is the acoustic compliance of the tympanic cavity. Tympanic cavity volume is approximately 0.04 cc, so that $C_t \approx 2.67 \times 10^{-8}$ cm⁵/dyn and $C_{eq} \approx 1.28 \times 10^{-8}$ cm⁵/dyn. Thus, $f_p \approx 5000$ Hz compared with the experimentally determined value of $f_p = 4500$ Hz in cat (Lynch, 1981). The difference is not significant considering that the cavity and foramen dimensions were roughly estimated from macerated skulls.

The following measurements were obtained from a skull of *Saimiri sciureus* (AMNH 93675):

Accessory cavity volume ≈ 0.12 cc

Tympanic cavity volume ≈ 0.04 cc

Foramen radius ≈ 0.03 cm

Foramen length ≈ 0.12 cm

Foramen geometry is complicated in *Saimiri* and most other platyrrhines and is not precisely described in terms of a length and a diameter; 0.03 cm is the radius of the narrow, foramen-like part of the aditus rostral to the preseptal recess. Thus, $f_s \approx 2000$ Hz and $f_p \approx 5000$ Hz as in *Tarsius*.

Beranek (1954) gives the acoustic impedance of an intermediate-sized tube as $Z_r = R_r + j\omega M_r$, where R is resistance. The ratio M_r/R_r is the "Q" of the resonant circuit and is a measure of the sharpness of the resonance curve. $R_r = (\rho/\pi r^2)(2\omega\mu)^{0.5}(L/r + 2)$, where ω = angular frequency ($2\pi f$) and μ = kinematic coefficient of viscosity ($0.156 \text{ cm}^2/\text{s}$ for air). For $f_s = 2000$ Hz, R_r is 205 ohms in *Tarsius* and 173 ohms in *Saimiri*. This compares to 10 ohms at 2125 Hz in cat (Lynch, 1981). The resonance is slightly sharper (has a narrower bandwidth) in the cat than in the primates. (See discussion in text.)

NOTE ADDED IN PROOF

Recent studies by Oster (1984; Sci. Amer. 250, pp. 108–114) indicate that the dominant frequency of muscle sounds is about 25 Hz, which may be too low to influence hearing in most species.

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